DTU Library

Blue carbon stocks in Baltic Sea eelgrass (Zostera marina) meadows

Rohr, Maria Emilia; Bostrom, Christoffer; Canal-Vergés, Paula; Holmer, Marianne

Published in:
Biogeosciences

Link to article, DOI:
10.5194/bg-13-6139-2016

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Rohr, M. E., Bostrom, C., Canal-Vergés, P., & Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (Zostera marina) meadows. *Biogeosciences*, *13*(22), 6139-6153. https://doi.org/10.5194/bg-13-6139-2016

Biogeosciences, 13, 6139–6153, 2016
www.biogeosciences.net/13/6139/2016/
doi:10.5194/bg-13-6139-2016

Biogeosciences Open Access EGU

Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows

Maria Emilia Röhr[1,2], Christoffer Boström[1], Paula Canal-Vergés[3], and Marianne Holmer[2]

[1]Åbo Akademi University, Faculty of Science and Engineering, Environmental and Marine Biology, Artillerigatan 6, 20520 Åbo, Finland
[2]University of Southern Denmark, Department of Biology, Campusvej 55, 5230 Odense M, Denmark
[3]Danish Shellfish Centre, DTU Aqua, Technical University of Denmark, Øroddevej 80, 7900 Nykøbing Mors, Denmark

Correspondence to: Maria Emilia Röhr (mrohr@abo.fi)

Received: 13 April 2016 – Published in Biogeosciences Discuss.: 27 April 2016
Revised: 9 October 2016 – Accepted: 15 October 2016 – Published: 14 November 2016

Abstract. Although seagrasses cover only a minor fraction of the ocean seafloor, their carbon sink capacity accounts for nearly one-fifth of the total oceanic carbon burial and thus play a critical structural and functional role in many coastal ecosystems. We sampled 10 eelgrass (*Zostera marina*) meadows in Finland and 10 in Denmark to explore seagrass carbon stocks (C_{org} stock) and carbon accumulation rates (C_{org} accumulation) in the Baltic Sea area. The study sites represent a gradient from sheltered to exposed locations in both regions to reflect expected minimum and maximum stocks and accumulation. The C_{org} stock integrated over the top 25 cm of the sediment averaged 627 g C m^{-2} in Finland, while in Denmark the average C_{org} stock was over 6 times higher (4324 g C m^{-2}). A conservative estimate of the total organic carbon pool in the regions ranged between 6.98 and 44.9 t C ha^{-1}. Our results suggest that the Finnish eelgrass meadows are minor carbon sinks compared to the Danish meadows, and that majority of the C_{org} produced in the Finnish meadows is exported. Our analysis further showed that > 40 % of the variation in the C_{org} stocks was explained by sediment characteristics, i.e. dry density, porosity and silt content. In addition, our analysis show that the root : shoot ratio of *Z. marina* explained > 12 % and the contribution of *Z. marina* detritus to the sediment surface C_{org} pool explained > 10 % of the variation in the C_{org} stocks. The mean monetary value for the present carbon storage and carbon sink capacity of eelgrass meadows in Finland and Denmark, were 281 and 1809 EUR ha^{-1}, respectively. For a more comprehensive picture of seagrass carbon storage capacity, we conclude that future blue carbon studies should, in a more integrative way, investigate the interactions between sediment biogeochemistry, seascape structure, plant species architecture and the hydrodynamic regime.

1 Introduction

Atmospheric carbon dioxide (CO_2) enters the ocean via gas-exchange processes at the ocean–atmosphere interface. In the ocean, dissolved inorganic carbon is fixed in photosynthesis by primary producers, and released again through respiration. A large percentage of this fixed carbon is stored and sequestered in the sediments of vegetated coastal ecosystems, of which the three globally most significant are salt marshes, mangrove forests and seagrass meadows (Herr et al., 2012). The carbon stored by these ecosystems is known as blue carbon (Duarte et al., 2005, 2013a; Nellemann et al., 2009). Blue carbon ecosystems function as carbon sinks, in which the rate of carbon sequestered by the ecosystem exceeds the rate of carbon lost through respiration and export.

Seagrass meadows play a critical structural and functional role in many coastal ecosystems (Orth et al., 2006). Although seagrass meadows only cover globally about 300 000–600 000 km^2 of the ocean sea floor, corresponding to 0.1 to 0.2 % of the total area, their carbon sink capacity (the capacity of seagrasses to absorb and store carbon in living and dead biomass and in the sediments) may account for up to 18 % of the total oceanic carbon burial (Gattuso et al., 1998; Duarte et al., 2005; Kennedy et al., 2010; Fourqurean et al., 2012). A large portion of the carbon sequestered (captured and stored) by seagrasses is stored in sediments, with a conservative value of 10 Pg C in the top 1 m of seagrass sediments (Fourqurean et al., 2012). Con-

Published by Copernicus Publications on behalf of the European Geosciences Union.

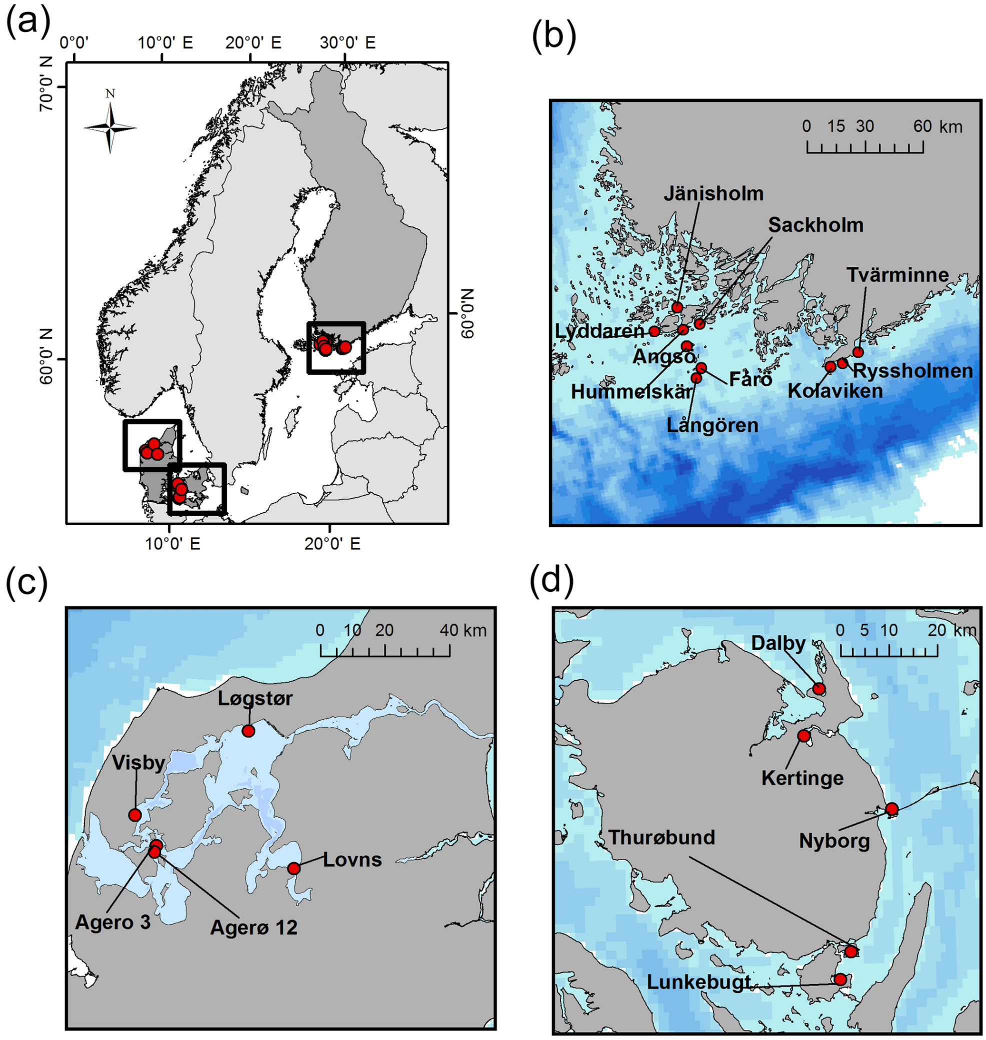

Figure 1. The study sites in Denmark and Finland. **(a)** Study regions, **(b)** Finnish study sites, **(c)** Limfjorden study sites, and **(d)** Funen study sites.

sequently, recent global estimates imply that seagrass sediments store almost 25 200 to 84 000 t C km^2 (Fourqurean et al., 2012). More importantly, carbon in submerged sediments is stored for timescales of millennia, while terrestrial soils are usually less stable and only sequester carbon up to decades (Hendriks et al., 2008).

The coasts of Scandinavia and the Baltic Sea are key distribution areas for eelgrass (*Zostera marina* L.) meadows (Boström et al., 2002, 2014). The meadows extend from fully saline (> 30) along the Norwegian coast to brackish (5–6) archipelago areas of Finland. This region is estimated to support > 6000 individual meadows covering at least 1500–2000 km^2, which is 4 times more than the combined eelgrass area of western Europe (Spalding et al., 2003; Boström et al., 2014). Consequently, this region plays a key role in the coastal carbon dynamics, but we presently lack estimates of the role of eelgrass for carbon storage in temperate sediments. Seagrasses are being lost at accelerating rates, and it has been estimated that 29 % of global seagrass area has disappeared since the initial recording of seagrasses in 1879 (Waycott et al., 2009). This decline could have severe consequences on the total capacity of marine ecosystems to store and sequester carbon in addition to the other ecosystem services seagrass meadows provide. Little is known about the magnitude of carbon emissions from degraded seagrasses ecosystems, not to mention its economic implications. A recent study shows that, despite the importance of these ecosystems in the global carbon budget, none of the three blue carbon ecosystems have been included in global carbon market protocols (Pendleton et al., 2012).

Seagrasses exhibit marked differences in shoot architecture and grow under variable environmental settings, making direct extrapolations between species and locations difficult. Consequently, there is a pressing need to better understand which factors are causing variability in carbon storage (C_{org} stocks, carbon stored in living and dead seagrass biomass and sediments) and the capacity of seagrass meadows to sequester carbon (C_{org} accumulation) in seagrass sediments. Indeed, recent studies show considerable influence of seagrass habitat setting, sediment characteristics and species-specific traits on the variability in carbon storage capacity in seagrass meadows (Duarte et al., 2013a; Lavery et al., 2013; Miyajima et al., 2015). Such differences contribute to uncertainty in local and global estimates of the carbon storage capacity and carbon dynamics in coastal seagrass areas.

In order to determine seagrass C_{org} stocks and C_{org} accumulation, knowledge on the sources of the carbon stored in the sediments is also crucial. The different C_{org} sources vary in their turnover compared to seagrasses (sources other than seagrasses being typically faster) and volumes of standing stock (typically less) and thus affect the dynamics of the C_{org} stocks and accumulation (Fry et al., 1977; Holmer et al., 2004; Kennedy et al., 2004, 2010). Seagrasses are known to be enriched in $\delta^{13}C$ compared to other potentially sources of C_{org} in the seagrass sediments, such as plankton, macroalgae, allochthonous carbon material, seagrass epiphytes, and benthic microalgae (Kennedy et al., 2004, 2010; Fry and Sherr, 1984; Moncreiff and Sullivan, 2001; Bouillon et al., 2003; Bouillon and Boschker, 2006; Macreadie et al., 2014). Thus, the stable isotope signals of seagrasses and other potential C_{org} sources can be relatively easily and reliably used as a proxy for identification of the origin of C_{org} in seagrass sediment carbon pool (Kennedy et al., 2010). Unfortunately, the current knowledge base on how these factors interact and influence carbon fluxes and storage is, at best, limited at both local and global scales.

In this study, we contrast storage, accumulation rates and sources of the accumulated carbon in eelgrass (*Zostera marina*) meadows in two regions differing in salinity, temperature and seagrass productivity, namely Finland and Denmark. Specifically, we asked the following questions:

1. How large is the carbon storage capacity (C_{org} stocks) of Baltic Sea eelgrass meadows?

2. What are the environmental factors determining the variability in carbon storage (C_{org} stocks) and accumulation (C_{org} accumulation) at local and regional scales?

3. How do the sediment characteristics influence the carbon storage (C_{org} stocks) of eelgrass meadows at local and regional scales?

4. How much carbon (C_{org} stocks) is presently stored in Finnish and Danish eelgrass meadows?

5. What is the present and historically lost (only in Denmark) monetary carbon value?

2 Materials and methods

2.1 Study area

Plant and sediment samples were collected in June–September 2014 from 10 sites in Finland (the Archipelago Sea) and 10 sites in Denmark (Funen and Limfjorden; Fig. 1). The Baltic Sea sediments are typically mineral sediments consisting of glaciofluvial deposits and only a small fraction of the sediment carbon content consists of carbonates (Leipe et al., 2011). The inorganic carbon content in our samples was low and contributed 0.5–5 % of total carbon content ($n = 10$ sites per region), and therefore carbonates were not removed from the sediment samples prior to the analysis to avoid analytical errors in low organic samples (Schlacher and Connolly, 2014). However, when interpreting the data it should be kept in mind that, given the %IC (inorganic carbon) variation in the samples for the different sites (range 0.1–5.78 %; average 3.33 %), the inorganic carbon could cause bias in the stable isotope signals of the sediment surface samples (range 0.16–1.17 ‰; average 0.76 ‰).

The study sites in each region spanned a gradient from sheltered to exposed areas. The Archipelago Sea of southwestern Finland is a shallow (mean depth 23 m), brackish (salinity 5–6) coastal area characterized by a complex mosaic of some 30 000 islands and skerries (Boström et al., 2006; Downie et al., 2013). The region is heavily influenced by human pressures, especially eutrophication, and exhibits naturally steep environmental gradients as well as strong seasonality in temperature and productivity (Boström et al., 2014).

Limfjorden is a brackish water area in the Jutland Peninsula connected to both North Sea and Kattegat with salinity ranging from 17 to 35. The fjord has a surface area of $\sim 1500\,km^2$ and a mean depth of 4.7 m (Olesen and Sand-jensen, 1994; Wiles et al., 2006; Petersen et al., 2013). Funen is located between the Belt Seas in the transition zone where waters from Baltic Sea and Kattegat meet. The salinity of the area ranges between 10 and 25 and the annual mean water temperature ranges from 10 to 15 °C (Rask et al., 1999). This study was conducted in shallow (< 10 m) fjords around Funen. The Danish areas are also heavily influenced by human pressures, especially eutrophication from intense agricultural farming (Ærtebjerg et al., 2003; DMU).

2.2 Field sampling

All samples were collected from depths of 2.5–3 m by scuba diving. At all sites, three replicate sediment cores (corer: length, 50 cm; diameter, 50 mm) were taken randomly at a minimum distance of 15 m from each other. The corer was manually forced to a depth of 30–40 cm and the sediment between 0 and 25 cm was used for the analysis. The cores were capped in both ends underwater and kept in a vertical position during transport to the laboratory. Eelgrass production and biomass were measured at all sites from four randomly chosen locations within the eelgrass meadow. In the vicinity of each sediment core, shoot density was counted using a 0.25 m^2 frame, and above- and belowground biomass samples were collected with a corer (diameter 19.7 cm) and bagged underwater. Additionally, when present, samples of plants and algae (drift algae, other angiosperms, phytoplankton and epiphytes) considered likely carbon sources in the eelgrass meadows were collected from each site for identification and analysis of stable isotope composition. Approximately 10 g of wet material was collected for each species. Annual eelgrass production was determined from estimates of previous growth by applying the horizontal rhizome elongation technique (Short and Duarte, 2001). From each site, five replicate rhizome samples with the longest possible intact rhizome carefully removed, collected and transported to the laboratory for further analysis.

2.3 Seagrass variables

In the laboratory, the above- and belowground biomass was separated, and eelgrass leaves and rhizomes were cleaned of epiphytes, detritus and fauna with freshwater and gently scraped with a scalpel. All plant material was dried to constant weight (48 h in 60 °C). The belowground biomass was separated into living and dead rhizomes and dried separately. Only the living rhizomes were used for the belowground biomass measurements, while samples of both living and dead rhizomes were used for analysis of organic carbon (OC) and stable isotopic composition of the organic carbon ($\delta^{13}C$). The root : shoot ratio was calculated as the ratio between below- and aboveground biomasses of *Z. marina* samples. A pooled sample of two youngest leaves from 10 randomly selected shoots were collected prior to drying from the aboveground biomass samples and dried separately for analysis of OC and $\delta^{13}C$. All samples were analysed by means of a Thermo Scientific Delta V Advantage isotope ratio mass spectrometer. The measured isotope ratios were represented using the δ notation with Vienna Pee Dee Belemnite as the reference material.

Determination of annual eelgrass production was done by measuring length of each individual internode of the rhizomes to the nearest millimetres. To obtain an estimate of the mean annual production per site, internode length measurements of individual replicates ($n = 5$) were pooled. Due to the lack of two annual production peaks in both regions, the annual production was estimated based on the distance between shortest and longest measured internodes, assuming that they represent the time point when the water temperature was at its minimum and maximum average, respectively. The time points for the water temperatures were obtained from databases of the Finnish and Danish meteorological institutes.

2.4 Sediment variables

In the laboratory, sediment samples were sliced into sections of 2–5 cm, where the upper 10 cm layer was divided into 2 cm layers and the remaining part into 5 cm layers. From each subsample, visible plant parts and fauna were removed before the sediment was homogenized. From the 0–2 cm section a subsample of 20 mL was taken for grain size analysis with a Malvern Mastersizer 3000 particle size analyser. The sediment silt content was calculated as the fraction with particle size of 2–63 µm from the range of all particle sizes (Folk and Ward, 1957). Sediment water content, dry bulk density and porosity were determined from a subsample of 5 mL that was taken using a cut-off 5 mL syringe and weighed before and after drying at 105 °C for 6 h from all sediment layers. The dried sediment samples were homogenized in a mortar and divided into two subsamples, of which one was used for analysis of sediment organic matter content (OM, as loss on ignition: 4 h at 520 °C) and the other for analysis of sediment $\delta^{13}C$ and OC as described above for the plant materials. Inorganic carbon content was low in sediments from both regions (< 5 %) and considered insignificant compared to the organic fraction (1–2 orders of magnitude higher).

2.5 C_{org} stock and C_{org} accumulation calculations

The depth-integrated C_{org} stocks were calculated according to Lavery et al. (2013) by multiplying the OC (OC mg g DW^{-1}) measured from different sections of the sediment core by the corresponding sediment dry density (g cm^{-3}). These numbers were then depth-integrated over 25 cm in order to estimate the depth-integrated carbon density. To estimate sediment C_{org} stock and C_{org} accumulation of Finnish and Danish eelgrass area, we used averages from 10 sites from each region in our calculations. The C_{org} (obtained by depth integration of the carbon density (mg C cm^{-3}) of the sampled region was multiplied by estimated seagrass area of the region based on the most recent areal estimates (in km^2) of seagrass distribution available in the literature (Boström et al., 2014) and given as C_{org} in g C m^{-2}. In Finland, the estimated areal extent was 30 km^2, while in Denmark the extrapolations were based on the minimum and maximum estimates of the areal extent, respectively (673 and 1345 km^2; Boström et al., 2014). Results for carbon accumulation (applied by multiplying the depth-integrated C_{org} stock by regional seagrass area and sediment accumulation rate estimate from the literature) in each area are given as C_{org} accumulation (t yr^{-1}). Due to the lack of long-term monitoring of sediment accumulation in eelgrass meadows, we used available minimum, average and maximum sediment accumulation rates in seagrass meadows obtained from the literature (Duarte et al., 2013b; Serrano et al., 2014; Miyajima et al., 2015).

To calculate the total C_{org} pool in Danish and Finnish eelgrass sediments, we summed the following three components: (1) the annual areal eelgrass carbon accumulation rate (C_{org} accumulation in $t\,C\,ha^{-1}\,yr^{-1}$, calculated by dividing the measured C_{org} stocks ($C\,g\,DW\,m^{-2}$) in each region by the time that it takes to accumulate this stock with a sedimentation rate of $2.02\,mm\,yr^{-1}$), (2) the total C in the average living aboveground and belowground *Z. marina* tissue ($t\,C\,ha^{-1}$), and (3) the mean C_{org} stocks ($t\,C\,ha^{-1}$) in eelgrass sediments in Denmark and Finland, respectively. To calculate the present and lost economic value of eelgrass carbon stocks, we used the social cost of carbon of $40.3\,EUR\,t\,C^{-1}$ (United States Government, 2010) and multiplied this value by the C_{org} stocks ($t\,C\,km^{-2}$). To estimate the Danish eelgrass losses over the past 100 years in economic terms, we used the calculations above, but accounted for the annually lost sequestration value by multiplying the rate by 100. We used the most recent loss estimates for Denmark for the period 1900–2000, assuming that the present coverage constitutes 10 or 20 % of the historical area (Boström et al., 2014).

2.6 Sediment carbon sources

The Isosource 1.3 isotope mixing model software (Phillips and Gregg, 2003) was used to estimate the contribution of different carbon sources to the sediment surface C_{org} stock. We ran the Isosource model using the $\delta^{13}C$ obtained from stable isotope analysis of *Z. marina* leaves and living and dead rhizomes, as well as for samples of other abundant C_{org} sources within the meadow ($n = 1$–5) with increments of 1 % and tolerance of 0.1. Numbers are given as percentage contribution to the sediment surface carbon pool.

2.7 Data analysis

All statistical analyses were performed using the PRIMER 6 PERMANOVA+ package (Anderson et al., 2008). A two-factor mixed model was used, in which sampling sites and region (FIN, DEN) were used as fixed factors for the biological response variable (sediment organic carbon stock, $g\,C\,m^{-2}$). In addition we ran reduced, country-wise DistLm models in order to better address the possible differences in regional environmental drivers for C_{org} stock. Prior to analysis, the environmental predictor variables (degree of sorting, sediment dry density, sediment water content, sediment porosity, sediment silt content, sediment organic content, annual production, root : shoot ratio, shoot density and percentage of *Z. marina* detritus contribution to C_{org}) were visually inspected for collinearity using draftsman plots of residuals. Due to autocorrelation between sediment variables (water content, porosity and dry density) sediment water content was removed from the environmental variables. To achieve normality in the retained environmental variables, data was log-transformed ($\log(X+1)$ and Euclidean distance was used to calculate the resemblance matrix. The biological response variable (C_{org} stock in $g\,C\,m^{-2}$) was square-root-transformed and Bray–Curtis similarity was used to calculate the abundance matrix. The relative importance of different environmental variables was determined by use of DistLm, a distance-based linear model procedure (Legendre and Anderson, 1999). The DistLm model was constructed using a stepwise procedure that allows addition and removal of terms after each step of the model construction. AICc (Akaike information criterion with a correction for finite sample sizes) was chosen as the information criterion as it enables fitting of the best explanatory environmental variables from a relatively small biological dataset compared to the number of environmental variables (Burnham and Anderson, 2002). An alpha level of significance of 95 % ($p < 0.05$) was used for all of the analysis. All means are reported as mean ±SE (SEM).

3 Results

3.1 Seagrass meadow and sediment characteristics

In general, the Finnish meadows were found on exposed sandy bottoms, while the environmental settings of the eelgrass meadows in Denmark were more variable (Fig. 2). Shoot density was nearly equal in both regions, averaging 417 ± 75 (shoots m^{-2}) in Finland and 418 ± 32 (shoots m^{-2}) in Denmark. In Finland, variation between sites (112–773 shoots m^{-2}) was greater than in Denmark (300–652 shoots m^{-2}). In Denmark the highest shoot density was found at the most exposed site (Nyborg), while in Finland the highest shoot density was found at Sackholm, a fairly sheltered site. The lowest shoot densities in Finland and Denmark were found in Tvärminne and Løgstør, respectively. The mean aboveground biomasses were 101 ± 3 and 145 ± 5 ($g\,DW\,m^{-2}$) and the mean belowground biomasses 79 ± 5 and 148 ± 13 g ($DW\,m^{-2}$) at Finnish and Danish sites, respectively. In Denmark, the mean fraction of OC in aboveground and belowground *Z. marina* tissue was 35 ± 0.32 and 29 ± 1.10 % DW, respectively, while the corresponding numbers for Finland were 38 ± 0.24 and 36 ± 0.27 % DW, respectively. Given an average total *Z. marina* biomass (above- and belowground) of 293 ± 22.31 (Denmark) and $180 \pm 9.60\,g\,DW\,m^{-2}$ (Finland), we estimate the C_{org} pool in bound in living seagrass biomass to 0.66 ± 0.005 and $0.94 \pm 0.014\,t\,C\,ha^{-1}$ in Finland and Denmark, respectively. The root : shoot ratio was slightly lower in Finland (0.87 ± 0.05) than in Denmark (1.14 ± 0.12), and varied from 0.29 to 3.29 and 0.15 to 6.45 in Finland and Denmark, respectively. The annual production of eelgrass for Finland (average $524 \pm 62\,g\,DW\,m^{-2}\,yr^{-1}$) showed relatively low variation between sites (270–$803\,g\,DW\,m^{-2}\,yr^{-1}$), being lowest at Jänisholm and highest at Ryssholmen. In Denmark, the mean annual eelgrass production was almost twice as high ($928 \pm 159\,g\,DW\,m^{-2}\,yr^{-1}$) with large variation ($470$–$2172\,g\,DW\,m^{-2}\,yr^{-1}$). Production was lowest and highest at Dalby and Visby, respectively (Table 1).

Table 1. Location, silt content (% silt), sediment dry density (Dry dens., g cm^{-3}), sediment organic carbon content (SedOC, % DW), sediment organic matter content (SedOM, % DW), $\delta^{13}C$ sediment surface, $\delta^{13}C$ *Z. marina* leaves, $\delta^{13}C$ *Z. marina* rhizomes, seagrass shoot density (Shoot density, shoots m^{-2}), seagrass above- and belowground biomass (AB and BB, g DW m^{-2}), root : shoot ratio ($R : S$), and aboveground production (Production, g DW m^{-2} yr^{-1}) at the sampling sites. SE ($n = 3$–4) is given. Annual seagrass production is calculated from pooled values of replicates per site and therefore no SE is shown.

Country/ location	Silt content (%)	Dry dens. (g cm^{-3})	SedOM (% DW)	SedOC (% DW)	$\delta^{13}C$ sediment surface	$\delta^{13}C$ *Z. marina* leaves	$\delta^{13}C$ *Z. marina* rhizomes	Shoot density (shoots m^{-2})	AB (g DW m^{-2})	BB (g DW m^{-2})	$R : S$	Production (g DW m^{-2} yr^{-1})
Finland												
Fårö	5.0 ± 1.4	1.32 ± 0.025	0.66 ± 0.07	0.13 ± 0.001	−20.6 ± 0.3	−9.7 ± 0.4	−9.0 ± 0.20	304 ± 32	138 ± 20	167 ± 28	1.27 ± 0.13	773
Hummelskär	9.0 ± 2.6	1.33 ± 0.009	1.06 ± 0.20	0.35 ± 0.019	−19.4 ± 1.2	−9.3 ± 0.3	−9.8 ± 0.25	364 ± 31	70 ± 11	28 ± 2	0.45 ± 0.06	446
Jänisholm	7.1 ± 2.1	1.37 ± 0.076	0.93 ± 0.20	0.33 ± 0.135	−22.1 ± 0.4	−10.8 ± 0.4	−11.0 ± 0.28	128 ± 17	65 ± 16	46 ± 2	1.44 ± 0.53	270
Kolaviken	1.9 ± 0.2	1.34 ± 0.035	0.75 ± 0.02	0.13 ± 0.011	−19.5 ± 0.2	−10.3 ± 0.3	−11.4 ± 0.34	476 ± 96	74 ± 6	149 ± 16	2.07 ± 0.27	324
Lyddaren	4.9 ± 2.5	1.34 ± 0.171	1.75 ± 0.70	0.45 ± 0.094	−13.5 ± 3.5	−8.8 ± 0.4	−9.6 ± 0.29	228 ± 42	86 ± 7	57 ± 12	0.64 ± 0.09	505
Långören	4.4 ± 2.1	1.42 ± 0.046	2.70 ± 2.10	0.19 ± 0.019	−18.9 ± 0.4	−8.5 ± 0.1	−8.9 ± 0.15	436 ± 53	121 ± 46	68 ± 25	0.58 ± 0.06	788
Ryssholmen	2.7 ± 0.6	1.34 ± 0.054	0.89 ± 0.20	0.16 ± 0.004	−20.7 ± 0.3	−11.5 ± 0.1	−11.5 ± 0.29	756 ± 57	160 ± 3	136 ± 16	0.86 ± 0.11	803
Sackholm	12.4 ± 1.9	1.36 ± 0.042	0.95 ± 0.20	0.26 ± 0.027	−21.1 ± 0.8	−10.3 ± 0.7	−9.9 ± 0.34	774 ± 234	110 ± 18	37 ± 9	0.31 ± 0.04	377
Tvärminne	9.2 ± 1.9	1.33 ± 0.034	0.88 ± 0.20	0.20 ± 0.016	−22.7 ± 0.6	−11.6 ± 0.1	−11.5 ± 0.25	112 ± 11	99 ± 16	38 ± 7	0.37 ± 0.01	436
Ängsö	6.3 ± 0.5	1.36 ± 0.052	0.84 ± 0.02	0.20 ± 0.010	−20.1 ± 0.3	−10.3 ± 0.1	−10.3 ± 0.28	604 ± 98	91 ± 6	63 ± 9	0.67 ± 0.05	521
FIN average	6.3 ± 1	1.35 ± 0.014	1.4 ± 0.3	0.24 ± 0.033	−19.9 ± 0.3	−10.1 ± 0.3	10.3 ± 0.32	417 ± 75	101 ± 3	79 ± 5	0.87 ± 0.06	524
Denmark												
Agero 3	29.4 ± 6.2	1.24 ± 0.085	1.94 ± 0.60	2.30 ± 0.082	−13.0 ± 1.7	−9.2 ± 0.5	−11.1 ± 0.22	448 ± 89	181 ± 33	84 ± 8	0.52 ± 0.07	1075
Agero 12	27.3 ± 7.7	1.35 ± 0.173	1.65 ± 0.80	0.29 ± 0.135	−17.4 ± 0.8	−10.7 ± 0.3	−11.9 ± 0.21	404 ± 90	110 ± 2	46 ± 9	0.40 ± 0.08	576
Dalby	8.1 ± 1.2	1.37 ± 0.034	0.67 ± 0.03	0.12 ± 0.009	−17.3 ± 0.7	−9.7 ± 0.3	−10.5 ± 0.56	400 ± 48	76 ± 7	83 ± 10	1.09 ± 0.11	470
Kertinge	27.1 ± 1.5	1.15 ± 0.045	12.59 ± 1.60	3.23 ± 0.236	−16.6 ± 0.2	−9.2 ± 0.1	−9.8 ± 0.08	328 ± 64	90 ± 17	64 ± 14	0.68 ± 0.02	527
Lovns	17.3 ± 2.7	1.22 ± 0.092	2.90 ± 0.50	1.53 ± 0.088	−16.3 ± 2.4	−11.5 ± 0.4	−12.2 ± 0.37	360 ± 27	141 ± 4	100 ± 11	0.70 ± 0.06	848
Lunkebugt	33.0 ± 7.4	1.23 ± 0.227	4.72 ± 2.40	1.71 ± 0.806	−16.9 ± 0.3	−8.9 ± 0.9	−10.6 ± 0.38	347 ± 81	210 ± 10	382 ± 24	1.82 ± 0.08	1056
Løgstør	4.0 ± 0.4	1.23 ± 0.025	0.75 ± 0.03	0.31 ± 0.089	−17.7 ± 0.4	−9.7 ± 0.4	−10.4 ± 0.51	300 ± 14	149 ± 11	63 ± 13	0.42 ± 0.07	755
Nyborg	0.5 ± 0.3	1.17 ± 0.027	0.42 ± 0.02	0.10 ± 0.006	−17.6 ± 1.1	−9.3 ± 0.2	−10.6 ± 0.34	652 ± 30	203 ± 24	214 ± 50	1.00 ± 0.14	1179
Thurøbund	34.6 ± 2.8	1.27 ± 0.030	14.48 ± 0.80	5.78 ± 0.512	−15.5 ± 0.4	−8.2 ± 0.1	−9.0 ± 0.22	420 ± 98	101 ± 16	398 ± 15	4.54 ± 0.70	619
Visby	21.0 ± 3.6	1.25 ± 0.021	1.17 ± 0.06	2.18 ± 0.201	−13.8 ± 1.2	12.0 ± 0.6	−12.4 ± 0.70	520 ± 21	193 ± 13	49 ± 4	0.25 ± 0.01	2172
DK average	20.2 ± 3.9	1.25 ± 0.022	3.9 ± 1.5	1.75 ± 0.563	−16.20 ± 0.2	−9.8 ± 0.4	−10.9 ± 0.33	418 ± 32	145 ± 5	148 ± 14	1.14 ± 0.13	928

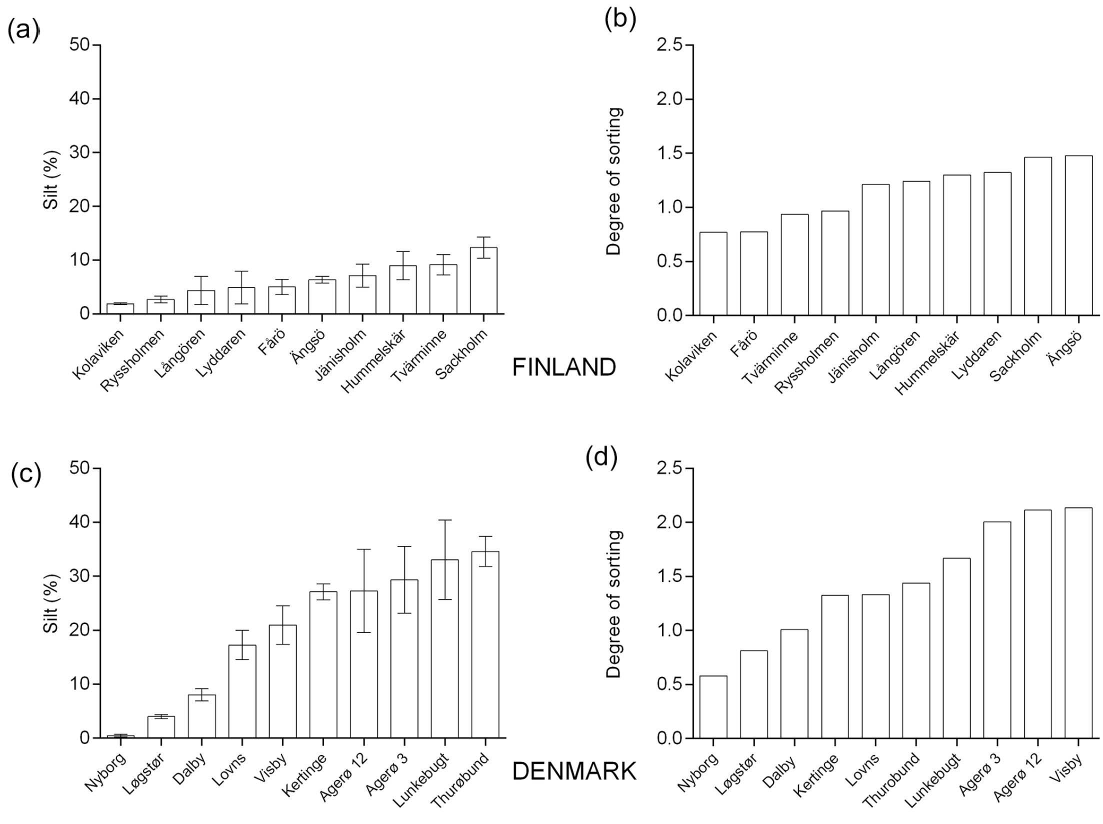

Figure 2. Silt content (%; **a**, **c**) and degree of sediment sorting **(b, d)** at the study sites in Finland and Denmark. Lower values in degree of sorting indicate well-sorted sediment types.

The sediment characteristics varied significantly between Finland and Denmark. There was a significant difference ($F_{1,9} = 14.7$, $p < 0.003$) between regions in terms of silt content, which was generally lower at Finnish (6.3 ± 1 %) sites than at Danish sites (20.2 ± 3.9 %), although in Denmark the variation between sites ranged from 0.8 % at Nyborg to 31.6 % at Thurøbund (Table 1, Fig. 2). In Finland, the variation between sites was lower and ranged from 1.6% (Kolaviken) to 15.5 % (Sackholm). At the Finnish sites the mean sediment dry density was higher (1.35 ± 0.01 g cm^{-3}) compared to the Danish sites (1.25 ± 0.02 g cm^{-3}), and the Finnish sites exhibited lower within-region variability, ranging from 1.1 g cm^{-3} at Lyddaren to 1.5 cm^{-3} at Långören, while the Danish sites varied from 0.3 g cm^{-3} at Thurøbund to 1.5 g cm^{-3} at Visby. The Finnish sites showed consistently lower pools of organic matter (LOI: 1.4 ± 0.3 % DW) compared to the average of Danish sites (LOI: 3.9 ± 1.5 % DW). Similarly, the mean OC content was lower in Finland (0.24 ± 0.033) than in Denmark (1.75 ± 0.563). Consequently, the mean water content was similarly lower in Finland (20.9 ± 0.4 %: range 16–29 %) than in Denmark (37.4 ± 1.8 %: range 17–76 %; Table 1). Sediment porosity was similar in both regions, ranging from 0.25 to 0.30 in Finland and from 0.20 to 0.40 in Denmark. At the Finnish sites, the proxy (degree of sorting) that was used to estimate exposure varied from 0.8 to 1.5 (φ), with Kolaviken being the most exposed site and Ängsö the most sheltered. In Denmark, the degree of sorting varied from 0.6 to 2.1 (φ), with Nyborg and Visby being the most exposed and sheltered sites, respectively (Fig. 2).

3.2 Organic carbon stocks

The profiles of carbon densities (g C cm^{-3}) in the upper 25 cm of the sediment showed marked differences both between and within the sampled regions. At the Finnish sites, where eelgrass typically grows at exposed locations, the sediment carbon density was low (mean 2.6 ± 0.09 mg C cm^{-3}) and declined with depth at most of the 10 study sites (Fig. 3). At the Danish sites, however, the sediment carbon density was more variable (mean 17.45 ± 9.42 mg C cm^{-3}) both within and between sites (Fig. 3). Depth-integrated C_{org} stocks (0–25 cm, g C m^{-2}, Fig. 4) were particularly high at one sheltered site in Funen, namely Thurøbund. This site is characterized by soft sediments with high organic content, high annual eelgrass production and high belowground biomass (Table 1). The lowest eelgrass C_{org} stocks in Denmark were found at two relatively exposed and sandy sites, namely Nyborg and Dalby (Fig. 4). The estimate of average total C_{org} stock in Finland was 0.019 ± 0.001 Mt C when taking the total area of eelgrass into account (30 km^2; Table 2). Using minimum and maximum estimates of the eelgrass area in Denmark, the estimates for mean total sediment C_{org} stock in Denmark were 2.164 ± 0.005 or 5.868 ± 0.014 Mt C, respectively (673 and 1345 km^2; Table 2).

Using an annual carbon accumulation value of 0.05 and 0.35 t C ha^{-1} yr^{-1} for Finland and Denmark, respectively, and assuming sediment accumulation of 2.02 mm yr^{-1} on average (Table 2), the total pool of C_{org} in the *Z. marina* meadows (C_{org} bound in living biomass, sediment C_{org} stock and C_{org} accumulation) corresponds to 6.98 t C ha^{-1} (698t km^{-2}) and 44.9 t C ha^{-1} (4490 t km^{-2}) for Finland and Denmark, respectively. Using the social cost of carbon of 40.3 EUR t C^{-1} (United States Government, 2010), the present economic value of eelgrass carbon in Finnish and Danish eelgrass meadows is estimated at 281 and 1809 EUR ha^{-1}, respectively. Using an average of these values (1045 EUR ha^{-1}) and a conservative estimate of the eelgrass acreage in the Baltic Sea (2100 km^2: Boström et al., 2014), we estimate a total monetary value of the present sequestration by eelgrass meadows to be EUR 219.4 million. Given the total eelgrass loss in Denmark for the time period 1900–2000 is between 5381 km^2 (present area 20 % of historical distribution) and 6053 km^2 (present area 10 % of historical distribution), this is equal to a C_{org} loss of 0.042 and 0.048 Gt C, respectively. Using the average value (1045 EUR ha^{-1}), these areal loss estimates correspond to a economic loss of between EUR 562 and 632 million for the minimum and maximum areal loss estimates, respectively.

3.3 C_{org} accumulation

The estimates for annual C_{org} accumulation in the Finnish seagrass meadows (30 km^2) were low (0.002, 0.016, 0.033 Mt C yr^{-1}), when applying sediment accumulation rates of 0.32, 2.02 and 4.20 mm yr^{-1}, respectively. The low C_{org} accumulation in Finnish meadows was a result of low mean C_{org} stocks and relatively small size of seagrass area compared to Denmark (Table 2). The estimates for annual C_{org} accumulation for the Danish sites differed between the two subregions Limfjorden (18 km^2) and Funen (179 km^2). At the sampling sites around Funen, the C_{org} accumulation was 0.139, 0.881 and 1.832 Mt C yr^{-1}, while in Limfjorden the C_{org} accumulation was lower (0.006, 0.038 and 0.079 Mt C yr^{-1}) and similar to C_{org} accumulation for Finland. Using upper and lower eelgrass areal estimates, total C_{org} accumulation based on three sediment accumulation rates in Denmark were more than 4 orders of magnitude higher (0.376, 2.373, 3.636 Mt C yr^{-1} and 0.75, 4.741 and 9.859 Mt C yr^{-1}) than the estimated total C_{org} accumulation in Finnish eelgrass meadows.

3.4 Carbon sources

The δ^{13}C values of the surface sediment within regions were quite homogeneous, ranging from -22.8 to -18.9 and -17.6 to 13.5 ‰ in Finland and Denmark respectively. The analytical error for the sediment δ^{13}C values was 2.8 %. The δ^{13}C in *Z. marina* tissues ranged from -11.4 to -8.5 and from -12.5 to -8.2 ‰, in Finland and Denmark, respectively. There was

Table 2. Estimated average carbon stocks (g C m^{-2} and Mt C), annual areal carbon accumulation (C_{org} acc. t C ha^{-1} yr^{-1}) and annual carbon accumulation (Annual C_{org}, Mt C yr^{-1}) in Finnish and Danish eelgrass (*Z. marina*) meadows. $Denmark_{lost}$: eelgrass area of the region lost since the beginning of the 1900s. $Limfjorden_{lost}$: eelgrass area of the region lost since the 1900s. See text for calculations. For calculations of annual carbon accumulation, three different sediment accumulation rates were applied (0.32 mm yr^{-1}; Miyayima et al., 2015; 2.02 mm yr^{-1}; Duarte et al., 2013b; and 4.2 mm yr^{-1}; Serrano et al., 2014), and for C_{org} seq. a sediment accumulation rate of 2.02 mm yr^{-1} was used.

Region	Seagrass area	Carbon density	C_{org} stock	C_{org} stock	C_{org} seq.	Annual C_{org} accumulation (Mt C yr^{-1})		
	(km^2)	(mg C cm^{-3})	(g C m^{-2})	(Mt C)	(t C ha^{-1} yr^{-1})	0.32 mm yr^{-1}	2.02 mm yr^{-1}	4.20 mm yr^{-1}
Finland	30	2.60 ± 0.09	627 ± 25	$0.019 \pm < 0.001$	0.052	0.002	0.016	0.0328
Limfjorden	18	10.57 ± 1.66	2644 ± 207	0.047 ± 0.007	0.213	0.006	0.038	0.079
Funen	179	24.32 ± 9.15	6005 ± 1127	1.090 ± 0.410	0.491	0.139	0.881	1.832
$Denmark_{min}$	673	17.45 ± 9.42*	4324 ± 1188*	2.164 ± 0.005	0.352	0.376	2.373	3.636
$Denmark_{max}$	1345	17.45 ± 9.42*	4324 ± 1188*	5.868 ± 0.014	0.352	0.75	4.741	9.859
$Denmark_{lost}$	5381–6230	17.45 ± 9.42*	17.45 ± 9.42*	23.478–27.183	n.d	n.d	n.d	n.d

* Mean carbon density (mg C cm^{-3}) calculated for Denmark is used. n.d: no data.

Table 3. Test statistics for DistLM analyses marginal tests.

Variable	SS	Pseudo-F	*P* value	Proportion
1. Root : shoot ratio	5309	10.64	0.002	0.155
2. Sediment dry density	10704	26.37	0.001	0.313
3. Annual eelgrass production	4959	9.82	0.002	0.145
4. Shoot density	48	0.08	0.911	0.001
5. Porosity	3507	6.61	0.010	0.102
6. Silt content (%)	12653	33.99	0.001	0.369
7. C : N ratio of plant material	464	0.79	0.397	0.014
8. *Z. marina* content (%)	12179	32.02	0.001	0.356
9. Degree of sorting	9725	23.01	0.001	0.284

no significant difference between living above- and below-ground tissue, and decomposed belowground tissue and samples were pooled in the isotope mixing model. Although *Z. marina* was the dominant seagrass species in Finland, the study sites included both monospecific and mixed seagrass meadows. Mixed meadows typically contained pondweeds, e.g. *Potamogeton pectinatus* and *Potamogeton perfoliatus*. In particular, *P. pectinatus* (δ^{13}C −11.3 to −7.6 ‰) and *P. perfoliatus* (δ^{13}C −15.6 to −12.6 ‰) were both present at five of the Finnish study sites (Jänisholm, Sackholm, Hummelskär, Tvärminne and Fårö) and *P. pectinatus* was present at Kolaviken, Ryssholmen and Lyddaren. *Ruppia cirrhosa* (−11.5 to −8.8 ‰) was less abundant and found at three of the Finnish sites (Sackholm, Ängsö, Kolaviken) and at one study site in Denmark (Kertinge). The δ^{13}C for phytoplankton ranged from −24.6 to −22.6 and −18.6 to 16.4 ‰ in Finland and Denmark, respectively. Drift algae was present at all Danish study sites except for Thurøbund and had δ^{13}C values from −17.9 to −13.5 ‰, but was only at five Finnish sites (Ängsö, Ryssholmen, Fårö, Långören and Hummelskär), with δ^{13}C values ranging from −20.0 to −16.3 ‰.

The isotope mixing model indicated that phytoplanktonic material was the major contributor (43–86 %) to the sediment surface C_{org} pool at all Finnish sites. In Denmark, *Z. marina* contributed 13–81 % to the sediment surface C_{org} pool, with the contribution being lowest at the most exposed site in Nyborg and highest in Visby. The corresponding numbers for Finland were 1.5–32 %, being lowest and highest in Tvärminne and Lyddaren, respectively (Fig. 5).

3.5 Environmental factors explaining carbon pools

The combined (FIN + DK) DistLm analysis showed that three sediment variables (dry density, silt content, porosity) and three plant variables (annual eelgrass production, the root : shoot ratio and *Z. marina* contribution to the sediment carbon pool) explained 67 % of the variation in the sediment C_{org} stock (g C m^{-2}; Tables 3 and 4, Fig. 6). Specifically, sediment silt content alone explained > 36 % of the variation in C_{org} stocks (Table 3). In both regions, exposed sites characterized by sandy, low organic sediments and low silt content had low C_{org} stocks. In contrast, at sheltered sites like Thurøbund in Denmark, we measured the highest sediment C_{org} stock along with highest silt and water content among all sites. Although sediment porosity and sediment dry density also contributed to the model, they were of minor importance (∼2 % each).

The combined (FIN + DK) DistLm analysis also showed that the *Z. marina* contribution to the sediment surface carbon pool explained 10.9 % of the variation in the measured C_{org} stocks (Fig. 6, Tables 3 and 4). Drift algae was a significant contributor (72 %) to the sediment surface C_{org} pool at the Danish sites, while it appeared to play only a minor role (0–21 %) in Finland. The carbon sources were generally more mixed at the Danish study sites compared to the Finnish sites where phytoplankton dominated (Fig. 5).

While the overall model including all sites explained almost 70 % of the variation in carbon stocks (Tables 3, 4) and indicated that the most relevant environmental variables were included in this Baltic-scale analysis, reduced, country-wise DistLM models revealed different results. In particular, variability in Finnish carbon stocks was explained up to 50 %

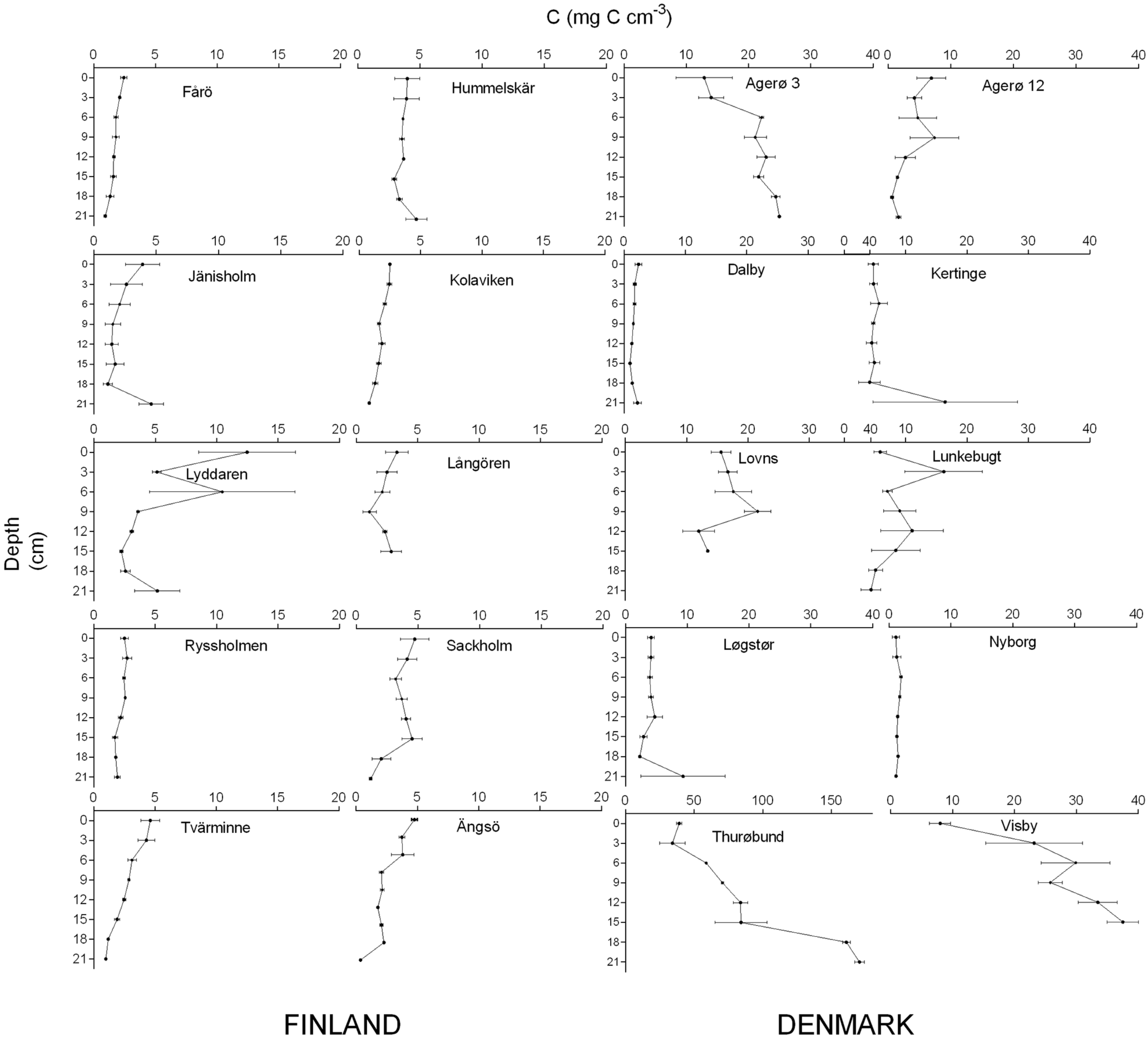

Figure 3. Sediment profiles of organic carbon density (mg C cm^{-3}) in the top 25 cm of the Finnish and Danish eelgrass (*Zostera marina*) meadows. Note the difference in the scale of x axis between the regions. Numbers below detection limit (% OC < 0.01 % DW) are not included in the figure. Average (±SEM; $n = 1$–3).

by geological variables (porosity, sorting and sediment dry density), while the best sequential model for carbon stock variability at Danish sites explained 75 % of the total variance. In contrast to Finland, the role of eelgrass-related variables (relative proportion of *Z. marina* in the sediment and the root : shoot ratio) was most important and explained 40 and 25 %, respectively, of the carbon stock variability.

4 Discussion

Recent studies have shown considerable variation in the global estimates of carbon stocks (C_{org} stocks) and carbon accumulation rates (C_{org} accumulation) in seagrass meadows, indicating an incomplete understanding of factors influencing this variability (Fourqurean et al., 2012; Duarte et al., 2013a; Lavery et al., 2013; Miyayima et al., 2015). The Baltic Sea forms a key distribution area for eelgrass in Europe, but similarly to the global data sets, we have so far

Table 4. Table from DistLm analysis showing results from the sequential tests and solution given by the analysis.

Variable	AICc	SS	Pseudo-F	P value	Proportion	Cumulative proportion	Degrees of freedom
Silt content (%)	357.4	12653	33.9	0.001	0.369	0.369	58
Root : shoot ratio	346.0	4375	14.5	0.001	0.127	0.497	57
Z. marina content (%)	333.6	3745	15.6	0.001	0.109	0.606	56
Production	332.2	805	3.5	0.037	0.023	0.630	55
Sediment dry density	331.3	700	3.2	0.049	0.020	0.650	54
Porosity	330.8	602	2.8	0.056	0.017	0.668	53
Best solution	AICc	R^2	RSS	Variables	Selections		
	330.8	0.668	11 363	6	1–3; 5; 6; 8		

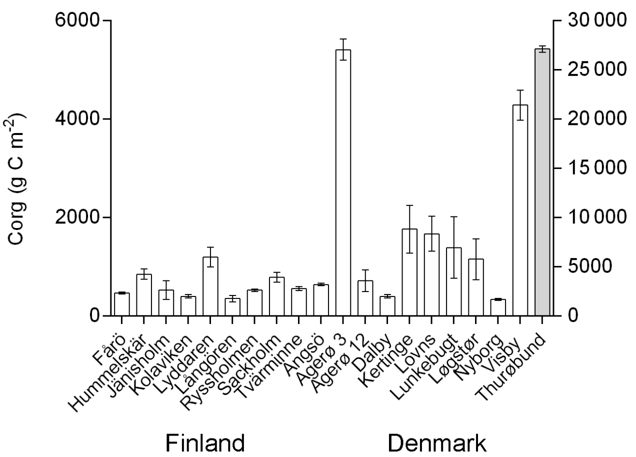

Figure 4. C_{org} stocks (g C m^{-2}) in the top 25 cm of sediment in Finnish and Danish eelgrass (*Zostera marina*) meadows. Note that the value of Thurøbund (grey bar) corresponds to the right y axis.

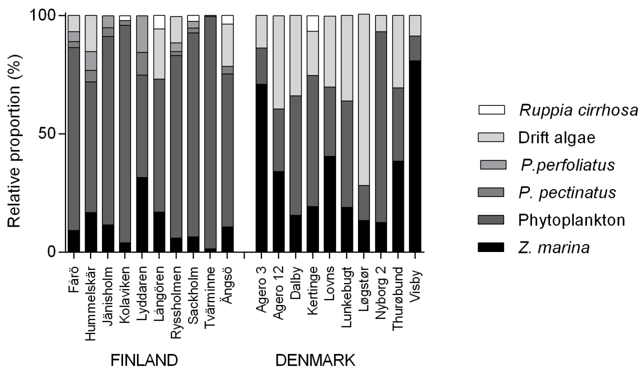

Figure 5. Relative contribution of different organic matter sources (*Z. marina*, *P. perfoliatus*, *P. pectinatus*, *Ruppia cirrhosa*, phytoplankton and drift algae) to the ^{13}C signal of the sediment surface layer (0–2 cm) in Finnish and Danish eelgrass (*Z. marina*) meadows.

lacked estimates on seagrass carbon stocks and accumulation.

In our study, the Finnish eelgrass meadows showed consistently very low C_{org} stocks and C_{org} accumulation, and the meadows were minor carbon sinks compared to the Danish meadows. The Danish sites showed more variation in the sediment C_{org} stock and accumulation, and C_{org} stock was particularly high at one site, Thurøbund (26 138 ± 385 g C m^{-2}), which is a relatively sheltered site with large amounts of organic sediments. Expectedly, due to both larger overall eelgrass acreage and larger C_{org} stocks in the Danish meadows, the total C_{org} accumulation (0.38–9.86 t C yr^{-1}) was 3 to 4 orders of magnitude higher than in the Finnish meadows (0.002–0.033 t C yr^{-1}). As eelgrass in Finland generally grows in more exposed locations, potentially due to increased interspecific competition with freshwater plants such as common reed (*Phragmites australis*) in sheltered locations (Boström et al., 2006), it is probable that most of the C_{org} produced in the Finnish meadows is exported and thus incorporated in detrital food webs in deeper bottoms. This argument is supported when applying sediment accumulation rates from the literature, as only 0.15–2.0 % of the annual production accumulated in Finnish meadows, while the corresponding numbers for Denmark were 0.6–7.8 %. Duarte and Cebrian (1996) estimated that on average 25 % of the global seagrass primary production is exported, and seagrass detritus may thus contribute significantly to C_{org} stocks in other locations, a fact that is often overlooked.

4.1 Extrinsic drivers of carbon sequestration in seagrass meadows

As proposed in previous work, accumulation of fine-grained size fractions in seagrass sediments, relative to those accumulated in bare sediments, appears to be one of the major factors influencing the carbon sink capacity of seagrass meadows (Kennedy et al., 2010; Miyajima et al., 2015) and may thus be a useful proxy for the sink capacity. In addition, it is well known that seagrasses modify sediments by reducing water flow and consequently increasing particle trapping and sedimentation and reducing resuspension (Fonseca and Fisher, 1986; Fonseca and Cahalan, 1992; Gacia et al., 2002; Hendriks et al., 2008; Boström et al., 2010).

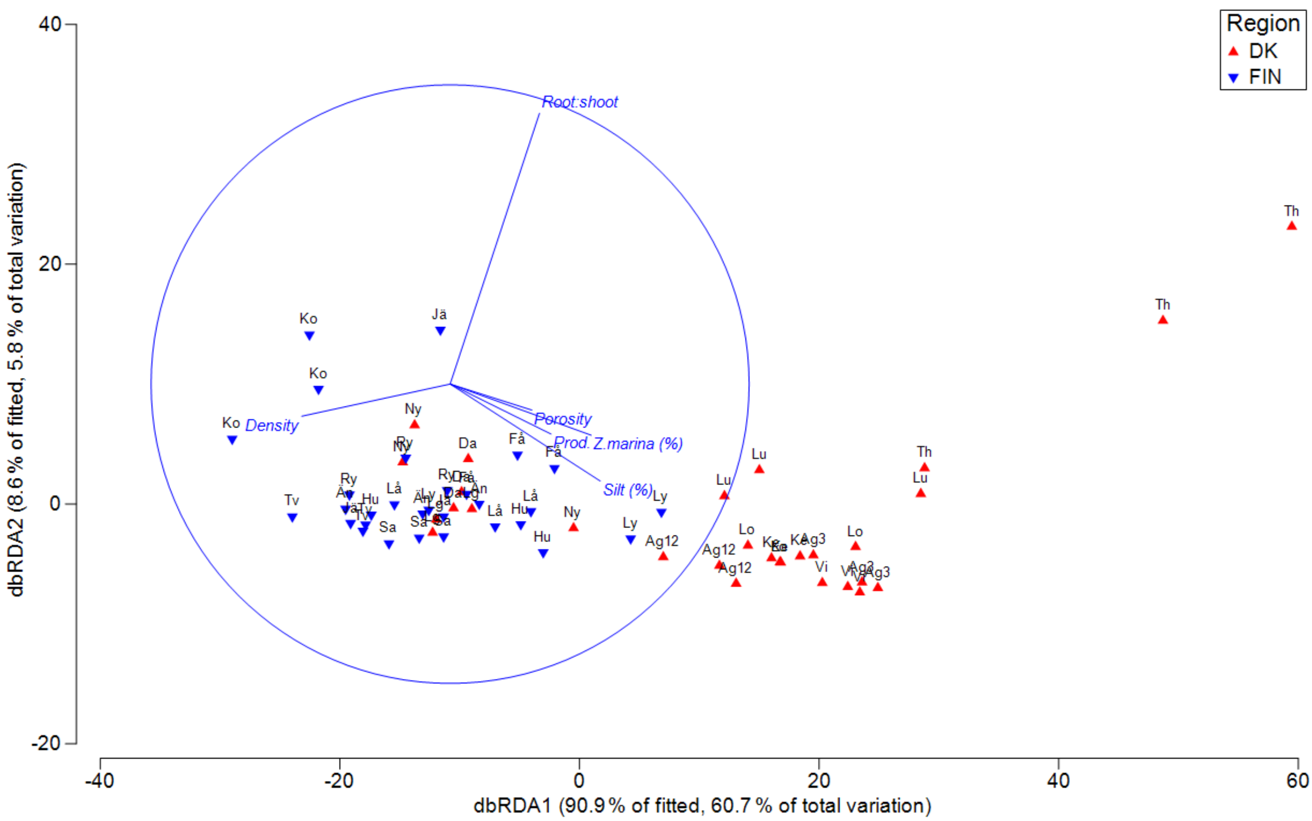

Figure 6. Distance-based redundancy analysis (dbRDA) plot showing the environmental parameters (percentage of *Z. marina* in sediment carbon pool, above : belowground ratio, annual eelgrass production, sediment silt content (%), sediment dry density and sediment porosity) fitted to the variation in the C_{org} stock ($g\,C\,m^{-2}$) at the Finnish and Danish eelgrass (*Z. marina*) sites. Vectors indicate direction of the parameters effect. Site codes for Finland – Ko: Kolaviken; Ry: Ryssholmen; Tv: Tvärminne; Få: Fårö; Ly: Lyddaren; Lå: Långören; Hu: Hummelskär; Jä: Jänisholm; Sa: Sackholm; Än: Ängsö. Site codes for Denmark – Ag12: Agerø12; Ag3: Agerø3; Vi: Visby; Lg: Løgstør; Lo: Lovns; Th: Thurøbund; Lu: Lunkebugt; Da: Dalby; Ke: Kertinge; Ny: Nyborg.

In this study, the DistLm analysis showed that contribution of *Z. marina* to the sediment surface carbon pool was an important driver (> 10.9 %) of the variation in the sediment C_{org} stock (Tables 3 and 4, Fig. 6) when the model included both regions. Surprisingly, the reduced country-wise analysis revealed different results and showed that *Z. marina* contribution to the sediment surface carbon pool was only an important driver for C_{org} stocks in Denmark. We believe that the country-wise differences in explanatory variables might relate to the more pronounced influence of eelgrass for carbon stocks at Danish sites. Indeed, these sites exhibited on average 30 % higher aboveground biomasses, 45 % higher belowground biomasses, 24 % higher root : shoot ratios and 44 % higher productivity compared to the Finnish sites. In Finland and the northern Baltic Sea, eelgrass meadows appears to be primarily physically controlled, and thus sediment variables play a relatively more pronounced role. The results from the model were also supported by our data, in which we found increasing C_{org} stocks at the Danish sites, where *Z. marina* was the major source of organic carbon, contributing 13–81 % to the surface sediment C_{org}, while in contrast, at the Finnish sites, where only a minor fraction of carbon buried in sediments derive from eelgrass detritus (1.5–39.6 %), the C_{org} stocks were low. Correspondingly, the average δ^{13}C value (−16.2 ‰) in the Danish sediment samples was similar to the global median value (−16.3 ± 0.2 ‰) reported by Kennedy et al. (2010), in which on average 51 % of the carbon was derived from seagrass detritus, whereas it was −20 ± 0.6 ‰ in Finland, indicative of higher contribution from other more negative carbon sources, such as phytoplankton. The importance of the *Z. marina* contribution to the C_{org} stocks may be explained by slow decomposition rates of seagrass tissue (54). In particular, the high proportion of refractory organic compounds in the seagrass belowground parts and high C : N : P ratios of seagrass tissue in general make seagrasses less biodegradable than most marine plants and algae (Fourqurean and Schrlau, 2003; Vichkovitten and Holmer, 2004; Kennedy and Björk, 2009; Holmer et al., 2011). The slow decomposition rates are also a result of reduced sediment conditions commonly encountered in Danish seagrass meadows (Kristensen and Holmer, 2001; Holmer et al., 2009; Pedersen et al., 2011). Despite the extensive distribution (2–29 ha), high biomasses (300–800 g DW m^{-2}) and major impact of drifting algal mats on coastal ecosystem functioning (Norkko and Bonsdorff, 1996; Salovius and Bonsdorff, 2004; Rasmussen et al., 2013; Gustafsson and Boström, 2014), the stable isotope composition of the sediments suggests that drift algae had a surprisingly minor influence on the sediment surface C_{org} pool in both regions. Thus, despite being present on several sampling sites, drift algae is likely exported and mineralized in deeper sedimentation basins. Furthermore, we found that, at all study sites in both regions, there were several other potential sources influencing the sediment surface C_{org} pool. Similarly, Bouillon et al. (2007) showed that, in seagrass sediments adjacent to mangrove forests in Kenya, none of their sites had seagrass material as the sole source of C_{org}, and instead mangrove-derived detritus contributed significantly to the seagrass sediment C_{org} pool.

Similarly to the contribution of *Z. marina* to the sediment surface carbon pool, the root : shoot ratio explained 12.7 % of the variation in the C_{org} stocks when both regions were included in the model; however, in the reduced country-wise models it was only an important driver for C_{org} stocks in Denmark. Accordingly, the highest C_{org} stocks, belowground biomass and root : shoot ratio were found in Thurøbund (Denmark). In Finland, the highest root : shoot ratio (2.07) was found at Kolaviken, with a relatively low C_{org} stock (397 g C m^{-2}). Due to the higher degree of exposure at the site (degree of sorting 0.7φ) compared to Thurøbund (1.4φ) it is likely that a large portion of the eelgrass production was exported away from the meadow and not stored in the sediment. The mean shoot densities were almost identical between regions, and shoot density did not contribute to the model explaining C_{org}.

The annual eelgrass production explained only 2.3 % of the variation in the C_{org} stocks in the combined model. The annual production rates were almost twice as high at Danish sites compared to the Finnish sites. Regional differences in seagrass productivity may be caused by differences in, for example, the inorganic carbon concentration in water column and light availability between the regions (with higher values in Denmark), which both affect the photosynthetic capacity of the plant (Hellblom and Björk, 1999; Holmer et al., 2009; Boström et al., 2014). Eelgrass production tends to be higher in physically exposed areas compared to more sheltered areas, which can be due to improved sediment oxygen conditions and hydrodynamical effects (Hemminga and Duarte, 2000). This finding was not supported by our study, in which we found the highest annual eelgrass production rates at both the most sheltered and most exposed sites, namely Visby and Nyborg (DK).

4.2 Geographical comparisons of carbon stocks and accumulation

Our estimated C_{org} stocks for the study sites were generally lower (627–4324 t C km^{-2}) than estimates (25 200–84 000 t C km^{-2}) found in the literature (Nelleman et al., 2009; Fourqurean et al., 2012). Several of the studies were conducted in the Mediterranean *P. oceanica* meadows – a habitat with superior carbon sequestration and storage capacity (Duarte et al., 2005; Lavery et al., 2013). The average sizes of C_{org} stocks in Finnish and Danish eelgrass meadows were also considerably lower than the mean values reported by Alongi (2014)for tropical seagrass meadows (14 270 t C km^{-2}). In contrast, our estimates for the carbon stock in the top 25 cm for Danish and Finnish meadows (627–6005 g C m^{-2}) are comparable to Australian (262–4833 g C m^{-2}: Lavery et al., 2013) and Asian estimates (3800–12 000 g C m^{-2}: Miyajima et al., 2015).

4.3 Consequences of seagrass loss for carbon pools

Despite the importance of seagrasses, their global distribution has decreased by 29 % since 1879 primarily due to anthropogenic pressures (Waycott et al., 2009), thus weakening the carbon sink capacity of marine environments to sequester carbon (Duarte et al., 2005). Since the 1970s, the Baltic Sea has been subject to strong anthropogenic pressures (Conley et al., 2009) leading to eelgrass declines in several countries (Boström et al., 2014). In the 1930s, the Danish eelgrass meadows were significantly reduced by the wasting disease (Rasmussen, 1977). These regime shifts in Denmark have resulted in a 80–90 % decline corresponding to 6726 km^2 in the beginning of the 1900s to 673–1345 km^2 in 2005 when using the minimum and maximum estimates for the current coverage area, respectively (Boström et al., 2014). Using the mean carbon density (17.45 mg C cm^{-3}) measured at the Danish sites, the lost C_{org} stock is estimated to be 23–27 Mt C, and these large-scale seagrass declines, which are also found in Sweden and Germany, have eroded the C_{org} stocks in the Baltic Sea significantly (Table 2). In Finland, there is a lack of long-term monitoring, but the meadows appear to be stable and cover at least 30 km^2 with no significant loss of C_{org} stocks.

Using a carbon monetary value of 40.3 EUR C^{-1}, we calculated the monetary value of the present carbon storage and sequestration capacity of eelgrass meadows in Finland and Denmark to be 281 and 1809 EUR ha^{-1}, respectively. Pendleton et al. (2012) calculated a global estimated economic cost of lost seagrass meadows to be USD 1.9–13.7 billion. This value was derived from the cost of lost carbon sink capacity, ignoring other lost ecosystem services, including coastal protection, water quality management, food provision and the role of seagrasses as fisheries and key habitats for marine species (Barbier et al., 2011; Atwood et al., 2015). Our estimate also only considers lost carbon sink capacity and can be compared directly with Pendleton et al. (2014). The present economic value of carbon storage and sequestration capacity of Baltic Sea eelgrass meadows is thus between 1.7 and 12 % out of the global seagrass blue carbon value.

While useful, our and previous work still remain snapshots of complex processes causing local and regional variability in estimates of seagrass blue carbon stocks and accumulation. Clearly, in order to produce more reliable estimates of global seagrass carbon sequestration rates and stocks, there is a need for more studies integrating and modelling the individual and joint role of, for example, sediment biogeochemistry, seascape structure, plant species architecture and hydrodynamic regime. Since seagrasses are lost at accelerating rates (Waycott et al., 2009), there is also an urgent need for a better understanding of the fate of lost seagrass carbon (Macreadie et al., 2014) and the development of the carbon sink capacity in restored seagrass ecosystems (Nellemann et al., 2009; Greiner et al., 2013; Marba et al., 2015). Nelleman et al. (2009) proposed the use of carbon trading programmes using financial incentives for forest conservation, such as REDD+ (Reduced Emissions from Deforestation and Degradation) and NAMAs (nationally appropriate mitigation actions), to include the blue carbon ecosystems as part of their environmental protection protocol. Both of these carbon mitigation programmes require ongoing monitoring of organic carbon storage and emission in the different blue carbon ecosystems. In order to manage seagrass meadows, mitigate climate change and produce information required for the carbon trading programmes, it is fundamental to understand factors influencing the capacity of seagrass meadows to capture and store carbon. By solving these uncertainties, the conservation and restoration of seagrass meadows can be implemented in the most beneficial manner by, for example, giving priority to protection of the seagrass meadows and species with the highest carbon sink capacity and foundation of restoration projects in areas most suitable for seagrass growth (Duarte et al., 2013a).

5 Data availability

The data are available from the corresponding author.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. This work is part of a double degree programme between Åbo Akademi University (ÅAU) and the University of Southern Denmark (SDU). The study was funded by the Maj and Tor Nessling Foundation (project 201600125: Baltic Sea blue carbon: environmental gradients influencing the carbon sink capacity of seagrass meadows) and the University of Southern Denmark. We acknowledge Archipelago Centre Korpoström and the University of Southern Denmark for excellent working facilities. Tiina Salo and Karine Gagnon are acknowledged for field assistance and Katrine Kierkegaard and Birthe Christensen for their assistance in the laboratory work.

Edited by: G. Herndl
Reviewed by: two anonymous referees

References

Alongi, D. M.: Carbon Cycling and Storage in Mangrove Forests, Annu. Rev. Mar. Sci., 6, 195–219, 2014.

Anderson, M. J., Gorley, R. N., and Clarke, K. R.: PERMANOVA for PRIMER: guide to software and statistical methods, Plymouth, UK, PRIMER-E Ltd., 2008.

Atwood, T. B., Connolly, R. M., Euan, G. R., Lovelock, C. E., Heithaus, M. R., and Hays, G. C, Predators help protect carbon stocks in blue carbon ecosystem, Nature Climate Change, doi:10.1038/NCLIMATE2763, 2015.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., and Silliman, B. R.: The value of estuarine and coastal ecosystem services, Ecol. Monogr., 81, 169–193, 2011.

Boström, C., Baden, S., Bockelmann, A., Dromph, K., Fredriksen, S., and Gustafsson, C.: Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems: implications for coastal management and conservation, Aq. Cons. Mar. Freshwater Ecosyst., 24, 410–434, 2014.

Boström, C., Törnroos, A., and Bonsdorff, E.: Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape, J. Exp. Mar. Biol. Ecol., 390, 106–117, 2010.

Boström, C., Bonsdorff, E., Kangas, P., and Norkko, A.: Long-term changes of a brackish-water eelgrass (Zostera marina L.) community indicate effects of coastal eutrophication, Estuar. Coast. Shelf Sci., 55, 795–804, 2002.

Boström, C., O'Brien, K., Roos, C., and Ekebom, J.: Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape, J. Exp. Mar. Biol. Ecol., 335, 52–73, 2006.

Bouillon, S. and Boschker, H. T. S.: Bacterial carbon sources in coastal sediments: a cross-system analysis based on stable isotope data of biomarkers, Biogeosciences, 3, 175–185, doi:10.5194/bg-3-175-2006, 2006.

Bouillon, S., Dahdouh-Guebas, F., Rao, A. V. V. S., Koedam, N., and Dehairs, F.: Sources of organic carbon in mangrove sediments: variability and possible ecological implications, Hydrobiologia, 495, 33–39, 2003.

Bouillon, S., Dehairs, F., Velimirov, B., Abril, G., and Borges, A. V.: Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi Bay, Kenya), J. Geophys. Res.-Biogeo., 112, G02018, doi:10.1029/2006JG000325, 2007.

Burnham, K. P. and Anderson, D. R.: Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach (2nd Edn.), Secaucus, NJ, USA, Springer, 2002.

Conley, D. J., Björck, S., Carstensen, J., Bonsdorff, E., Destouni, G., and Gustafsson,42, 3412–3418, doi:10.1021/es802762, 2009.

Ærtebjerg, G., Andersen, J. H., and Hansen, O. S. (Eds.): Nutrients and Eutrophication in Danish Marine Waters, A Challenge for Science and Management, National Environmental Research Institute, Denmark, 2003.

Downie, A., von Numers, M., and Boström, C.: Influence of model selection on the predicted distribution of the seagrass Zostera marina, Estuar. Coast. Shelf S., 121, 8–19, 2013.

Duarte, C. M. and Cebrian, J.: The fate of marine autotrophic production, Limnol. Oceanogr., 41, 1758–1766, 1996.

Duarte, C. M., Middelburg, J. J., and Caraco, N.: Major role of marine vegetation on the oceanic carbon cycle, Biogeosciences, 2, 1–8, doi:10.5194/bg-2-1-2005, 2005.

Duarte, C. M., Kennedy, H., Marba, N., and Hendriks, I.: Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies, Ocean Coast Man., 83, 32–38, 2013a.

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., and Marba, N.: The role of coastal plant communities for climate change mitigation and adaptation, Nature Climate Change, 3, 961–968, 2013b.

Folk, R. L. and Ward, W. C.: Brazos river bar: a study of significance of grain size parameters, J. Sediment Petrol., 27, 3–26 doi:10.1306/74D70646-2B21-11D7-8648000102C1865D, 1957.

Fonseca, M. S. and Fisher, J. S.: A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration, Mar. Ecol.-Prog. Ser., 29, 15–22, 1986.

Fonseca, M. S. and Cahalan, J. A.: A preliminary evaluation of wave attenuation by four species of seagrass, Estuar. Coast. Shelf Sc., 35, 565–576, 1992.

Fourqurean, J. W. and Schrlau, J. E.: Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA, Chem. Ecol., 19, 373–390, 2003.

Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marba, N., Holmer, M., and Mateo, A. M.: Seagrass ecosystems as a globally significant carbon stock, Nat. Geosci., 5, 505–509, 2012.

Fry, B. and Sherr, E. B.: d13C measurements as indicators of carbon flow in marine and freshwater ecosystems, Contrib. Mar. Sci., 68, 196–229, 1984.

Fry, B., Scalan, R. S., and Parker, P. L.: Stable Carbon Isotope Evidence for 2 Sources of Organic-Matter in Coastal Sediments – Seagrasses and Plankton, Geochim. Cosmochim. Ac., 41, 1875–1877, 1977.

Gacia, E., Duarte, C. M., and Middelburg, J. J.: Carbon and nutrient deposition in a Mediterranean seagrass (Posidonia oceanica) meadow, Limnol. Oceanogr., 47, 23–32, 2002.

Gattuso. J. P., Frankignoulle, M., and Wollast R.: Carbon and carbonate metabolism in coastal aquatic ecosystems, Annu. Rev. Ecol. Syst., 29, 405–434, 1998.

Greiner, J. T., McGlathery, K. J., Gunnell, J., and McKee, B. A.: Seagrass Restoration Enhances "Blue Carbon" Sequestration in Coastal Waters, Plos One, 8, e72469, doi:10.1371/journal.pone.0072469, 2013.

Gustafsson, C. and Boström, C.: Algal mats reduce eelgrass (Zostera marina L.) growth in mixed and monospecific meadows, J. Exp. Mar. Biol. Ecol., 461, 85–92, 2014.

Hellblom, F. and Björk, M. : Photosynthetic responses in Zostera marina to decreasing salinity, inorganic carbon content and osmolality, Aquat. Bot., 65, 97–104, 1999.

Hemminga, M. A and Duarte, C. D.: Seagrass Ecology, Cambridge University Press, Cambridge, UK, 2000.

Hendriks, I. E., Sintes, T., Bouma, T. J., and Duarte, C. M.: Experimental assessment and modeling evaluation of the effects of the seagrass Posidonia oceanica on flow and particle trapping, Mar. Ecol.-Prog. Ser., 356, 163–173, 2008.

Herr, D., Pidgeon, E., and Laffoley, D. (Eds.): Blue Carbon, Policy Framework: Based on the Discussion of the International Blue, Carbon PolicyWorking Group, IUCN and Arlington, Gland, Switzerland, USA, 39 pp., 2012.

Holmer, M., Duarte, C. M., Boschker, H. T. S., and Barron, C.: Carbon cycling and bacterial carbon sources in pristine and impacted Mediterranean seagrass sediments, Aquat. Microb. Ecol., 36, 227–237, 2004.

Holmer, M., Baden, S., Boström, C., and Moksnes, P.-O.: Regional variation in eelgrass (Zostera marina) morphology, production and stable sulfur isotopic composition along the Baltic Sea and Skagerrak coasts, Aquat. Bot., 91, 303–310, 2009.

Holmer, M.: Productivity and biogeochemical cycling in seagrass ecosystems, in: Coastal Wetlands: An Integrated Ecosystem Approach, edited by: Perillo, G. M. E., Wolanski, E., Cahoon, D. R., and Brinson, M. M., Amsterdam, The Netherlands, 377–401, 2009.

Holmer, M., Wirachwong, P., and Thomsen, M. S.: Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species, Mar. Biol., 158, 297–309, 2011.

Kennedy, H., Gacia, E., Kennedy, D. P., Papadimitriou, S., and Duarte, C. M.: Organic carbon sources to SE Asian coastal sediments, Estuar. Coast. Shelf S., 60, 59–68, 2004.

Kennedy, H. and Björk, M.: Seagrasses, in The Management of Natural Coastal Carbon Sinks in Coastal Ecosystems: Investigating and Realising the Potential, 2009.

Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., and Marba, N.: Seagrass sediments as a global carbon sink: Isotopic constraints, Global Biogeochem. Cy., 24, GB4026, doi:10.1029/2010GB003848, 2010.

Kristensen, E. and Holmer, M.: Decomposition of plant materials in marine sediment exposed to different electron accepters (O_2, NO_3^-, and SO_4^{2-}), with emphasis on substrate origin, degradation kinetics, and the role of bioturbation, Geochim. Cosmochim. Ac., 65, 419–433, 2001.

Lavery, P. S., Mateo, M., Serrano, O., and Rozaimi, M.: Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service, Plos One, 8, e73748, doi:10.1371/journal.pone.0073748, 2013.

Legendre, P. and Anderson, M. J.: Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments, Ecol. Monogr., 69, 512–512, 1999.

Leipe, T., Tauber, F., Vallius, H., Virtasalo, J., Uścinowicz, S., Kowalski, N., Hille, S., Lindgren, S., and Myllyvirta, T.: Particulate organic carbon (POC) in surface sediments of the Baltic Sea, Geo-Mar. Lett., 31, 175–188,2011.

Macreadie, P. I., Baird, M. E., Trevathan-Tackett, S. M., Larkum, A. W. D., and Ralph, P. J.: Quantifying and modelling the carbon sequestration capacity of seagrass meadows, A critical assessment, Mar. Pollut. Bull., 83, 430–439, 2014.

Marba, N., Arias-Ortiz, A., Masque, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J., and Duarte, C. M.: Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks, J. Ecol., 103, 296–302, 2015.

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Adachi, H., and Yamano, H.: Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows, Global Biogeochem. Cy., 29, 397–415, 2015.

Moncreiff, C. A. and Sullivan, M. J.: Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses, Mar. Ecol.-Prog. Ser., 215, 93–106, 2001.

Nellemann, C., Corcoran, E., Duarte, C. M., Valdés, L., De Young, C., and Fonseca, L.: Blue Carbon, A Rapid Response Assessment, 2009.

Norkko, A. and Bonsdorff, E.: Rapid zoobenthic community responses to accumulations of drifting algae, Mar. Ecol.-Prog. Ser., 131, 143–157, 1996.

Olesen, B. and Sandjensen, K.: Patch Dynamics of Eelgrass Zostera marina, Mar. Ecol.-Prog. Ser., 106, 147–156, 1994.

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., and Heck Jr., K. L.: A global crisis for seagrass ecosystems, Bioscience, 56, 987–996, 2006.

Pedersen, M. Ø., Serrano, O., Mateo, M. A., and Holmer, M.: Temperature effects on decomposition of a Posidonia oceanica mat, Aquat. Microb. Ecol., 65, 169–182, 2011.

Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., and Sifleet, S.: Estimating Global "Blue Carbon" Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems, Plos One, 7, e43542, doi:10.1371/journal.pone.0043542, 2012.

Petersen, J. K., Maar, M., Ysebaert, T., and Herman, P. M. J.: Near-bed gradients in particles and nutrients above a mussel bed in the Limfjorden: influence of physical mixing and mussel filtration, Mar. Ecol.-Prog. Ser., 490, 137–146, 2013.

Phillips, D. L. and Gregg, J. W.: Source partitioning using stable isotopes: coping with too many sources, Oecologia, 136, 261–269, 2003.

Rask, N., Pedersen, S. E., and Jensen, M. H.: Response to lowered nutrient discharges in the coastal waters around the island of Funen, Denmark, Hydrobiologia, 393, 69–81, doi:10.1023/A:1003510405699, 1999.

Rasmussen, E.: The wasting disease of eelgrass Zostera marina and its effects on environmental factors and fauna, Seagrass ecosystems, A scientific perspective, New York, Marcel Dekker Inc., 1977.

Rasmussen, J. R., Pedersen, M. F., Olesen, B., Nielsen, S. L., and Pedersen, T. M.: Temporal and spatial dynamics of ephemeral drift-algae in eelgrass Zostera marina, beds, Estuar. Coast. Shelf S., 119, 167–175, 2013.

Salovius, S. and Bonsdorff, E.: Effects of depth, sediment and grazers on the degradation of drifting filamentous algae (*Cladophora glomerata* and *Pilayella littoralis*), J. Exp. Mar. Biol. Ecol., 298, 93–109, 2004.

Schlacher, T. A. and Conolly, R. M.: Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis, Methods Ecol. Evol., 5, 541–550, 2014.

Serrano, O., Lavery, P. S., Rozaimi, M., and Mateo, A. M.: Influence of water depth on the carbon sequestration capacity of seagrasses, Global Biogeochem. Cy., 28, 950–961, 2014.

Short, F. and Duarte, C. M.: Methods for the measurement of seagrass growth and production., edited by: Short, F. T. and Cole, R. G., Global seagrass research methods Amsterdam: Elsevier, 155–182, 2001.

Spalding, M., Taylor, M., Ravilious, C., Short, F., and Green, E.: Global overview: The distribution and status of seagrasses, edited by: Green, E. P. and Short, F. T., in: World Atlas of Seagrasses: Present Status and Future Conservation, Berkeley California: University of California Press, 5–26, 2003.

United States Government: Technical Support Document, Social Cost of Carbon for Regulatory Impact Analysis Under Executive Order 12866 (United States Government Interagency Working Group on Social Cost of Carbon, Washington, DC), 2010.

Vichkovitten, T. and Holmer, M.: Contribution of plant carbohydrates to sedimentary carbon mineralization, Org. Geochem., 35, 1053–1066, 2004.

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., and Olyarnik, S.: Accelerating loss of seagrasses across the globe threatens coastal ecosystems, P. Natl. Acad. Sci. USA, 106, 12377–12381, 2009.

Wiles, P. J., van Duren, L. A., Hase, C., Larsen, J., and Simpson, J. H.: Stratification and mixing in the Limfjorden in relation to mussel culture, J. Mar. Syst., 60, 129–143, 2006.